MODULAR CIRCUITRY FOR COMBINING AND CONTROLLING DEGREES OF FREEDOM IN THE LIMB

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Abstract-**Work in the frog spinal cord, and more recently in mammals, suggests that the degrees of freedom problem in motor planning may be simplified by building motor actions from combinations of motor primitives. How motor primitives arise from spinal circuits, their properties and their plasticity are important issues for this framework. We have tested properties of primitives using various physiological perturbations in simple behaviors, and used various decomposition techniques (independent components analysis, matching pursuit cosine packet analysis, wavelet methods) in both simple and complex behaviors to examine the muscles that are controlled as groups or units, and to investigate the pattern and time scale of action of primitives in behaviors. Our work suggests that, for primitives organized in the spinal cord of the frog, modifications of time scale (e.g. temporal duration of primitives) in both simple spinal (e.g. wipe/scratch) and complex behaviors (e.g. struggling) are imposed or enabled by mechanisms residing above spinal cord in the medulla, suggesting a heterarchical control of the primitives in spinal cord. In the absence of medulla, spinal cord operates with a relatively fixed timing of the spinal primitives.**
Keywords - **primitives; force-fields; heterarchy; modularity**

I. INTRODUCTION

The notion that motor behavior, at least at a low level of execution details, might be described as a combination of a small number of modular controllers or primitives is an attractive one. Such a framework would provide a partial solution to Bernstein's degrees of freedom (DOFs) problem by coalescing the many joints and actuators of the biological musculoskeletal plant into a few control elements. This would simplify construction of reactive behaviors at low levels of the central nervous system (CNS) such as the segmental spinal cord reflexes. In addition the elements could form both a basis and a set of constraints for sensory motor integration and sensor fusion. Studies from many laboratories over many years have provided varying levels of support for such modularity. We have examined this question in the spinal cord of frogs isolated from the remaining CNS. These experiments support a decomposition of reflex behaviors into a set of primitives that specify multi-joint mechanical properties in the limb. The action of the primitive can be expressed as a visco-elastic force-field. Primitives could be combined in microstimulation by vector superposition [1-5]. Recently we have managed to examine combination in the more natural context of reflex behaviors of spinalized frogs [1-3]. Here we also found both combination and boolean decisions occuring. The goal of this paper is to review these data on spinal movement construction, discuss the control circuitry and architecture these data may suggest, and discuss

the ways we speculate these may be extended by descending controls.

II. METHODOLOGY

1) Force-field construction and microstimulation

Our initial examination of spinal motor output used microstimulation of the intermediate spinal cord grey matter in the spinalized frog. The grey matter can be likened to the circuitry and processing units of spinal cord, while the white matter is the cabling between circuit modules and the brain and body. Small current pulses (1-10 uA) recruited cells in a 50-100um radius in the grey matter (about 1000 cells). The motor patterns recruited by this stimulation and their isometric forces were recorded. An ATI 3/10 gamma type 6 axis force sensor was rigidly attached at the frog's ankle. The limb in this arrangement had 3 degrees of freedom at the hip, and one at the knee. The forces were fully described by a 3D translational force vector at the ankle attachment and a torque about the axis connecting sensor attachment and hip center. To describe the output as a force-field we needed to make force sensor measurements over the workspace of the limb while the same stimulation was applied to the same spinal cord site. We moved the ankle (and attached sensor) using a manipulandum. Forces at each ankle location were treated as samples from a force-field which evolved through time following stimulation. To estimate forces at arbitrary locations within the confines of the convex hull defined by the sample patterning we used, we constructed a tesselation using the Delaunay triangulation algorithm in either 2D or 3D. We then used a linear interpolator in each triangle or tetrahedron of the tesselation to provide an estimation of forces at a chosen location from the time matched vertex forces. In this way we described the results of stimuli as a time varying force-field.

In experiments of this type we found across all tested sites we could identify about 4-6 force patterns which had constant form over time i.e. force patterns could be expressed in the form:

$$\theta(r, \dot{r}, t) = A.a(t)\phi_i(r, \dot{r})$$

(1)

Where A was amplitude parameter related to the stimulus and a(t) a temporal pattern describing the evolution of the field. The velocity term was zero since the measurements were isometric. The a(t) in microstimulation were either (1) pulsatile (2) plateau (or step-like) or (3) pulse-step like. By scaling the stimulus the parameter A could be controlled.

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Abstract

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$\phi_i(\ r\ )$, constant over time represented the primitive.

2) Force-field collection in reflex behaviors

Although microstimulation may allow future novel technologies for functional electrical stimulation or other neuroprosthesis applications, to the physiologist this technique is rightly seen as highly artificial and far from the normal function of spinal cord. Therefore we also used the same force-field framework to examine spinal frog's motor production in reflex behaviors. The frogs were immobilized as previously and the fields measured by moving the limb to different locations while repeatedly eliciting the reflexes. The forces measured in this case represented attempted motions to known targets. Normal free-limb torque patterns could be obtained from free limb kinematics through inverse dynamics computations. As previously field patterns were collected. We found data in these experiments most often matched the description in equation (1) within a phase of movement. Force-field descriptions thus gave a parsimonious account of these data (see below).

3) Electromyogram collection and alnalysis including free-limb behavior

Marr's breakdown of issues in neural control and computation into a task level description, an algorithm level description and an implementation level description is particularly relevant in our methodology here. Even if force-field descriptions give a parsimonious account of the computation and constructions for motion, nonetheless the implementation details underlying this must be far more complex and could take many forms. Thus we also examined the neuromuscular activations themselves. These were recorded as electromyograms (EMG) in both free limb motion, perturbed motion and isometric conditions. These records allowed us to examine the patterns of muscles recruited in each case, the balance of amplitudes of recruited muscles, and relation of force patterns and movement generating torques to neural output. These data were particularly important to begin to link the force-level description to the neural circuitry and patterns of feedback regulation in the spinal cord.

4) Hypotheses tested

We have focussed on two sets of hypotheses. First, that at the spinal level motion is planned and executed as combinations of fixed duration force-field primitives. More precisely:

$$F(r,\dot{r},t) = \sum_i A_i\, a(t + \tau_i\,)\phi_i(r,\dot{r})$$

(2)

Where the spinal set comprises n primitives ϕ_i of similar activation dynamics $a(t)$. The task of spinal cord is to select amplitude A_i and phasing τ_i for each primitive ϕ_i to plan and modify execution as necessary. Thus a correction initiated on obstacle collision might recruit an ith primitive into the motor execution (see below).

Second, we also hypothesize that descending controls must augment the spinal system. We speculate this may happen in one of two ways :

(1) descending controls may modify spinal primitives using time dilations of primitives, combined with structural modifications.

$$F(r,\dot{r},t) = \sum_i A_i\, a(b_i t + \tau_i\,)\mu_i(\phi_i(r,\dot{r}))$$

(3)

Where b_i is a time dilation or frequency modulation of the primitive by descending control and μ_i is a modulation or warping function applied to the field structure by descending controls.

(2) higher CNS levels may augment the spinally organized set of elements by adding new primitives :

$$F(r,\dot{r},t) = \sum_i A_i\, a(t + \tau_i\,)\phi_i(r,\dot{r}) + \sum B_j\, b(t + \tau_j\,)\psi_j(r,\dot{r})$$

(4)

where ϕ_i are the spinal primitives and the Ψ_j are added novel primitives organized in higher CNS. $b_j(t+\tau_j)$ are their phasing and time courses and B_j their amplitude scalings.

III. RESULTS

A. Spinal construction of movement

We found in a series of experiments on spinal reflex organization reported in [1,2,3] that our data from spinal frogs were consistent with Equations 1 and 2 above. In both spontaneous omissions of groups of muscles [3] and in the effects of deafferentation and adjustment based on workspace location [1] muscle groups and force patterns were adjusted or deleted in a modular fashion.

B. On-line correction of movements

We also found in a study of collision induced corrective movements that corrections could be described as the recruitment in a modular fashion of a single primitive [2]. This primitive had a fixed time course (i.e. fixed a(t) in Eq. 2) regardless of when the collision occurred and when it was recruited. However the EMG and associated force-field was amplitude scaled based on the impact strength (i.e. A was varied in Eq.2). The primitive was combined with the ongoing motor pattern by superposition. In addition, the primitive was only recruited into the pattern within an initial time window in the motor pattern during which it could be effective, otherwise the impact with the obstacle elicited no added response. On the border of this time window, when the

primitive was recruited, failures of correction could occur. This was because a primitive normally recruited into the pattern at this time made the recruitment of the correction response primitive ineffective. The force patterns and actions of the two primitives were in opposition along a critical task dimension.

C. Issues in the organization of control of primitives

Future issues in the organization of primitives are as follows: First we need to understand the types of stability, and guarantees of these, provided by using a set of primitives. These issues are reviewed in [6,7]. In Slotine and Lohmiller [7] a detailed account of the development of contracting system analysis and its application to motor control is provided. Their analysis shows a collection of primitives of the correct form (contracting) can be used in development of complex parallel, hierarchical and feedback arrangements that continue to provide guarantees of contracting system behavior.

One interesting possibility to be considered is that the combination of motoneuron recruitment dynamics, the viscoelastic properties of muscle, and perhaps the operation of the monosynaptic reflex arc, provide a building block (the single muscle actuator) which is intrinsically a contracting system. The need for such a building block in a variety of tasks and framework is very well described in their review.

The individual muscle and its recruitment apparatus could indeed form the most fundamental contracting primitive. However, this description of motor organization avoids the issue raised in the Introduction of the degrees of freedom problem as it is faced in development and learning [see 6]. The high dimensionality of the musculoskeletal system provide an enormous search space. Further, the primitives found in our work above comprise collections of muscles and feedback controls. These appear to remain intact across tasks and have specific recruitment dynamics in spinal frogs. They provide multi-joint patterns that simplify the computational task of motor planning and execution. It is also likely they provide various stability guarantees e.g. by emulating a passive system, and perhaps fullfilling contracting system criteria. In the context of the degrees of freedom problem the issues then become, in our thinking, what the biomechanical and circuit structure of multi-joint primitives should be to (1) support fundamental reflex behavior, (2) allow rapid and simple adjustments of the reflex systems motor patterns to novel conditions and (3) provide a framework and bootstrap for the vast task space. In the context of 3 it is important to provide a circuitry that allows rapid design and elaboration of controls spanning areas of the task space, by adjustments and extension of the basis set. This would allow context dependent optimization, motor learning and novel task construction, and ultimately might provide control of individual muscles (fractionated muscle control) if needed.

D. Reflex control systems and primitives

We have begun to address the circuit structures that support multi-joint primitives by using muscle vibration to recruit the muscle spindle system (muscle length and velocity feedback) and the golgi tendon system (muscle force feedback) in individual muscles. In particular we are interested to discover if feedback systems (a) operate so as to respect primitives as units or (b) go beyond the confines of groups of muscles constituting primitives in ways that begin to breakdown the separations into primitives. In particular we are examining the idea that all feedback should preserve muscle recruitment ratios within primitives. Thus homonymous and heteronymous feedback gains from Ia systems should be scaled to preserve these ratios among all muscles comprising a primitive, and sensory information exchanged between primitives should affect primitives as a whole, not individual muscles. This idea thus makes strong predictions about the patterning and relations of elements in matrices describing the multi-joint multi-muscle feedback gain. To date our results continue to support this idea and the notion of a low level spinal circuitry organized around constructing and regulating primitives.

E. Pattern generators and primitives: speculations

Primitives have been examined somewhat separately from pattern generators [but see 1,2,3] where relations of motor patterns and rhythmic elements are beginning to be tested. Our data in reflex movements leads us to propose a functional analysis of the cord as a set of rhythm and phase generators, a computational system using both phase and limb state to select and recruit primitives, and a collection of primitives. The extent to which this function analysis can be mapped to separate circuit elements is completely unknown. The likelihood is that the rhythm and decision functions are both emergent from a distributed circuitry, although our analysis of primitives may support some dedicated circuit organization. It is important to distinguish the idea of dedicated circuits from the idea of
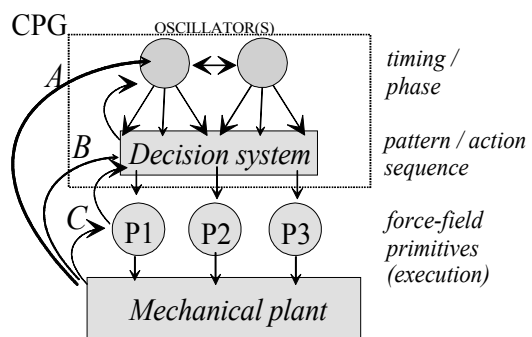

Fig. 1. Conceptual scheme of motion organization in spinal cord based on data collected in spinal frogs. A CPG comprises rhythm generation and a decision system for computation and planning of actions and contingency actions based on timing information and limb state. This layer recruits a collection of multi-joint force-field primitives during execution A,B and C: feedback information flow.
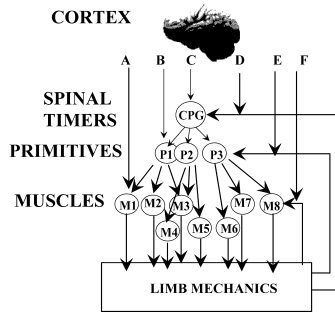
Fig.2. Sites of control and modification of primitives and CPG by descending controls. Each matches terms in Eq. 3 and 4 in the text. A and F: Creation of novel primitives by directly recruiting muscles or altering feedback organization (Eq. 4). B : direct use of spinal primitive. E modification of spinal primitive (Eq. 3). C,D modification of CPG by direct control or modulation of rhythm generation, or decision computations (Fig.1), or modulation of feedback phase resetting effects.

topographically distinct regions of spinal cord. The dedicated circuits could be either topographic or broadly distributed. This remains an open question. The scheme we currently use as our working hypothesis is described in Fig. 1.

F. Descending controls and primitives: extension of the basis

We speculate that descending controls may modify the system in Fig. 1 at several levels (Fig. 2), corresponding to different parameters in Eq. 3 and 4. Our most recent EMG data, collected in frogs with medulla intact, but remaining CNS destroyed, indicates that medullary controls allow time
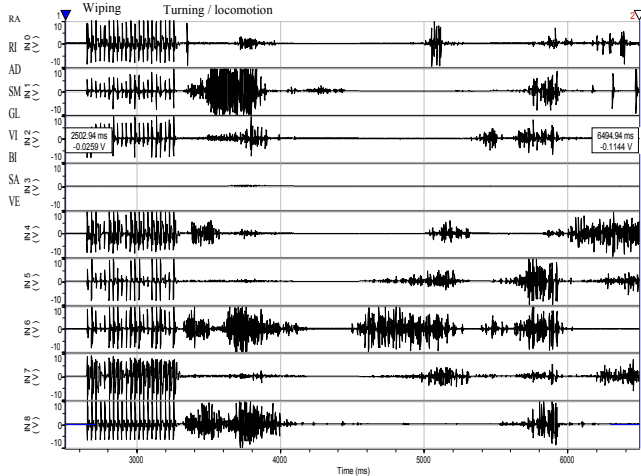

Fig. 3. Ranges of frequency in EMG activity in a frog with medullary descending influences on spinal cord. The range of burst durations is much greater than seen in spinal cord alone.

dilations of primitives to be used in a range of behaviors, including wiping reflex. This is at least one component of the increased flexibility of the preparation with medulla intact. These preparations exhibit persistent and flexible struggling, and directed kicking across a wider range of workspace, compared to the spinal frog with equivalent stimuli.An example of EMG from such a frog is shown in Fig. 3.

IV. CONCLUSION

The analysis of spinal reflex behavior as a collection of force-field primitives provides a parsimonious account of the planning and execution processes. However, the extent to which this description reflects the underlying neural structure is an area of active investigation fraught with difficulties [see e.g. 9,10]. Critical aspects of this investigation are first the relation of neural feedback and pattern generating circuits to primitives and their integrated operation, and second how the spinal systems are augmented, extended and adapted by descending controls. At least one aspect of these descending controls are modification of time scales of primitives and current data indicates the medulla plays an important role in this process.

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